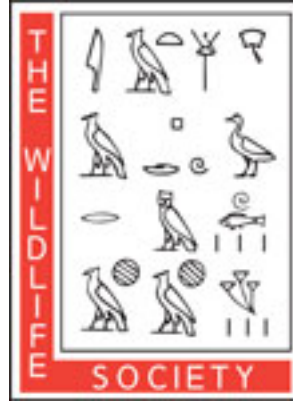


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Author(s): Theodore G. Chapin, Daniel J. Harrison and David M. Phillips

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# SEASONAL HABITAT SELECTION BY MARTEN IN AN UNTRAPPED FOREST PRESERVE

THEODORE G. CHAPIN,<sup>1</sup> Department of Wildlife Ecology, University of Maine, Orono, ME 04469-5755, USA

DANIEL J. HARRISON, Department of Wildlife Ecology, University of Maine, Orono, ME 04469-5755, USA

DAVID M. PHILLIPS, Department of Wildlife Ecology, University of Maine, Orono, ME 04469-5755, USA

**Abstract:** American marten (*Martes americana*) are often associated with mature conifer-dominated forests; however, marten may require complex vertical and horizontal woody structure, rather than a coniferous overstory. To evaluate whether marten prefer forests with a mature conifer overstory, we investigated landscape- and stand-scale habitat selection of 38 (20 M, 18 F) resident ( $\geq 25$  locations collected during  $\geq 3$  months), nonjuvenile ( $\geq 1$  year [YR]) marten in a forest preserve in northcentral Maine where trapping and timber harvesting had been excluded for  $> 35$  years. At the landscape scale, nearly all of the available habitat was used by marten. Further, composition of forest types within home ranges of radiocollared resident marten was similar to areas outside of home ranges. At the stand scale, marten used forest types disproportionately ( $P = 0.03$ ) from availability within their home ranges during summer (1 May–31 Oct), but exhibited no apparent selection ( $P = 0.83$ ) during winter. During summer, stands with substantial spruce-budworm (*Choristoneura fumiferana*)-caused mortality ( $< 50\%$  overstory canopy closure) had the highest selection index. No significant difference in stand-scale selection was detected among mature, well-stocked coniferous, deciduous, or mixed forest types during summer or winter. Mature, well-stocked coniferous forest was the least abundant forest type in home ranges of both sexes in both seasons, whereas mature, well-stocked deciduous forest was the most abundant. Further, much variability was observed in the amount of coniferous (range 0.8–36.3%) and deciduous (range 6.3–66.1%) habitat occurring in marten home ranges. Nine of 10 adult females captured in late spring were lactating, despite that their home ranges composed only 3–36% (median = 10.5%) mature coniferous forest. Our results suggest that marten do not require a dense or coniferous forest overstory and are consistent with the hypothesis that vertical and horizontal structure may be more important habitat components than age or species composition of the forest overstory. Thus, forest practices, such as on-site delimbing, cull-tree retention, and slash management may provide opportunities to maintain use of regenerating forest habitat by marten after harvesting. Structural complexity often may be associated with age and species composition of forests; however, conservation practices should consider structural attributes that functionally influence the quality of forested habitats for marten, rather than merely age, species composition, and canopy closure of the forest overstory.

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**Key words:** American marten, *Choristoneura fumiferana*, forest, habitat, Maine, *Martes americana*, preserve, selection, spruce budworm, structure, trapping.

American marten frequently have been reported as associates of late-successional coniferous or conifer-dominated mixed forests (Strickland et al. 1982b, Clark et al. 1987, Strickland and Douglas 1987, Thompson 1988, Buskirk and Powell 1994). Although dominant tree species vary across the range of marten, nowhere have marten been reported to select deciduous forests over forests with a substantial conifer component (Buskirk and Ruggiero 1994:22). The association of marten with coniferous forests seems strongest in the western United States (Koehler and Hornocker 1977,

Spencer et al. 1983, Buskirk et al. 1989, Wilbert 1992), where marten are considered indicator species of late-successional habitats in many national forests (Buskirk and Ruggiero 1994:9).

In northeastern North America, marten occupy areas with an abundance of deciduous and deciduous-dominated mixed forests (Francis and Stephenson 1972, Steventon and Major 1982, Taylor and Abrey 1982, Brown 1986, Katnik 1992). Still, some eastern studies (Francis and Stephenson 1972, Taylor and Abrey 1982, Wynne and Sherburne 1984) also have reported selection for coniferous forests, whereas others (Soutiere 1979, Bateman 1986, Katnik 1992) have reported selection for mixed coniferous-deciduous forests. Using scale-specific methodologies similar to those of our study, Katnik

<sup>1</sup> Present address: Ecology and Environment, Inc., Buffalo Corporate Center, 368 Pleasant View Drive, Lancaster, NY 14086, USA.

(1992) observed no significant differences in landscape- or stand-scale selection between deciduous and coniferous forest types or between well-stocked (>50% canopy closure) and poorly-stocked (<50% canopy closure) forest types in an industrial forest study site in Maine.

From 1980 to 1984, Maine supported nearly 50% of the annual harvest of marten in the conterminous United States (Novak et al. 1987). In 1982 the range of marten in Maine, 70% of which is owned by the forest products industry, was composed of 51% spruce-fir, and 28% deciduous forest (Powell and Dickson 1984). Timber supply models for Maine, based on a 1980 inventory, predicted a shortage of harvestable spruce-fir and deciduous forest by 2100 (Seymour and Lemin 1989). Hence, the characteristics of forested habitats selected by marten will have important implications for marten conservation in Maine, as well as in other parts of the species' range where land use alters the age and species composition of forests.

Some previous studies have suggested that marten require at least 30–50% canopy closure (Thompson and Harestad 1994:357); however, evidence suggests that forest canopy closure per se is not required by marten (Streeter and Braun 1968, Magoun and Vernam 1986). Indeed, recent literature reviews of marten habitat associations support the hypothesis that forest structure may be a more important habitat component than species composition of the forest overstory (Buskirk and Powell 1994:286, Buskirk and Ruggiero 1994:22). Coarse woody debris (CWD) on or near the forest floor may provide escape cover, thermally efficient resting sites in winter (Buskirk et al. 1989, Taylor 1993), and subnivean access to prey (Corn and Raphael 1992). In Maine, from 1974 to 1984, extensive outbreaks of spruce budworm, a native Lepidopteran, resulted in mortality of spruce (*Picea* spp.) and especially balsam fir (*Abies balsamea*) over large areas (Irland et al. 1988). This has caused profound changes in stands previously dominated by mature conifers, including reduced canopy closure and increased windfalls, snags, CWD, and deciduous, coniferous, and herbaceous regeneration. Previous studies in areas with severe spruce-budworm-caused mortality of trees (Wynne and Sherburne 1984) have not considered the influence of this natural disturbance on marten habitat associations.

Most previous studies of habitat selection by

marten were conducted in areas with timber harvesting, trapping, or both. However, the effects of timber harvesting and trapping may combine to reduce marten populations in timber-harvested areas (Thompson 1991, Hodgman et al. 1994), through habitat degradation and increased access for trappers via forest roads (Soukkala 1983, Hodgman et al. 1994). Indeed, several studies have documented lower densities of marten in cut versus uncut forests (Soutiere 1979, Snyder and Bissonette 1987, Phillips 1994, Thompson 1994), but results are confounded by uncontrolled variables (e.g., trapping pressure, prey densities), in addition to differences in forest characteristics that may influence marten density. Further, Van Horne (1983) cautioned that density may be a poor indicator of habitat quality without concurrent measures of population performance. A younger age structure, greater predation, and a lower pregnancy rate for female marten, each an indication of lower population performance, have been reported for cut versus uncut forests (Thompson 1994). However, in a comparison of density and indices of population performance between a trapped industrial forest and an untrapped forest preserve, Phillips (1994) reported that, although density was lower in the extensively clearcut landscape, lactation rates, home range size, and degree of spatial overlap did not differ among adult females between sites. Females on the industrial forest site studied by Phillips (1994) may have positioned their home ranges in areas with similar habitat quality compared with females in the adjacent forest preserve. Differences in density between the sites were associated with a smaller percentage of the landscape occupied and with trapping-caused mortality in the industrial forest. Hence, information about habitat selection by marten in an untrapped, mature-forest landscape will provide a baseline for comparisons with trapped, timber-harvested landscapes.

We investigated seasonal habitat selection by resident, nonjuvenile marten at both the landscape and stand scales in the absence of recent trapping (>50 YR) and timber harvesting (>35 YR) in northcentral Maine. Our primary objective was to evaluate whether marten exhibit selection for forest cover types in an area without recent trapping or timber harvesting. We incorporated spruce-budworm-caused mortality of trees, which resulted in <50% canopy closure, into our classification of forest types to account

for structural variation among forest types. We used a statistical approach to analyze selection that avoided pseudoreplication by treating the animal rather than individual relocations as the sampling unit. This approach also allowed for variability in selection among individuals and accounted for the spatial scale at which habitat use and availability were measured. We compared our results to those from a study of an adjacent population that inhabited an industrial forest with intensive trapping (Hodgman et al. 1994, Katnik 1992). To evaluate minimum and maximum thresholds for specific forest types within marten home ranges, we measured the composition of forest types within home ranges occupied by resident marten. Finally, to investigate the effect of age (i.e., reproductive status) on home range occupancy relative to forest-type composition, we compared the amount of coniferous and deciduous forest in home ranges of adult versus yearling male and female marten.

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## STUDY AREA

The study area was located in Nesourdnhunk Township (T5 R10 WELS) in Piscataquis County, Maine, in the westcentral portion of Baxter State Park. The portion of the Park that was closed to trapping and hunting extended for 3 km to the north, 10 km to the east, and 18 km to the south of the study area. An industrial forest owned by Great Northern Paper Company was adjacent to the western edge of our

study area and was characterized by extensive timber harvesting and intensive marten trapping (Hodgman et al. 1994). The study area was about 55 km<sup>2</sup>, with elevations from 330 to 735 m. Mean maximum July temperature for the region was 25 C, and mean minimum January temperature was -17 C (McMahon 1990). Average annual snowfall for the region was 300 cm, the highest in Maine (McMahon 1990).

Most of Baxter State Park has been managed as a wilderness preserve without trapping or timber harvesting since about 1960. Before legal protection, large-diameter spruce (*Picea* spp.) and eastern white pines (*Pinus strobus*) were removed selectively from the study area, resulting in a mosaic of naturally-disturbed stands regenerating from spruce-budworm mortality and mature stands dominated by deciduous and mixed deciduous-coniferous forest types. Mature stands were generally 70–100 years old with some individual trees >120 years old. A spruce-budworm epidemic from 1974 to 1984 (Irland et al. 1988) caused mortality of coniferous trees, especially balsam fir, resulting in stands with reduced canopy closure and apparent increases in snags, stumps, root masses, logs, and coniferous, deciduous, and herbaceous regeneration.

Conifer stands were dominated by balsam fir and red spruce (*Picea rubens*) and included eastern white pine, eastern hemlock (*Tsuga canadensis*), black spruce (*Picea mariana*), northern white cedar (*Thuja occidentalis*), and larch (*Larix laricina*). Deciduous stands included sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula allegheniensis*), paper birch (*B. papyrifera*), aspen (*Populus* spp.), and American beech (*Fagus grandifolia*). The understory in stands regenerating from extensive spruce-budworm mortality was dominated by balsam fir, maples (*Acer saccharum*, *A. rubrum*, and *A. pensylvanicum*), birches (*Betula* spp.), American mountain-ash (*Pyrus americana*), and raspberry (*Rubus* spp.), depending on site conditions.

## METHODS

### Capture and Telemetry

Marten were live-trapped, radiocollared, and radiotracked from 1 November 1990 to 30 April 1994 with the protocol described in Phillips (1994). Our capture and handling protocol was approved by the Institutional Animal Care and

Use Committee at the University of Maine, Orono. We extracted a first premolar tooth from all radiocollared marten to determine age using cementum annuli (Strickland et al. 1982a). We also extracted both lower canines from all dead radiocollared marten that we recovered and verified age using radiographs (Dix and Strickland 1986). During summer (1 May–31 Oct), we located marten every 12–36 hours from the ground and every 7–10 days from a fixed-wing aircraft. From the ground, locations were obtained with triangulation of  $\geq 2$  bearings from known positions, with  $>60^\circ$  and  $<130^\circ$  between the outermost bearings and separated in time by  $<30$  minutes. We used program TRIANG (White and Garrott 1984) to compute the coordinates and size of the error polygon for each location. From a fixed-wing aircraft, telemetry was conducted with 2 side-facing H-antennas and methods described by Gilmer et al. (1981). Observers recorded locations in flight on United States Geological Survey 7.5-minute topographic maps.

We measured angular error of observers using telemetry from fixed sites as the mean difference between true and estimated bearings to hidden transmitters. We used angular errors in program TRIANG (White and Garrott 1984) to compute the size of the error polygon for each relocation. Based on a comparison of mean telemetry error polygon with mean habitat polygon size (Nams 1989), we used locations with error polygons  $<25$  ha to define 95% minimum convex polygon (MCP) home ranges and used locations with error polygons  $<10$  ha to determine the specific forest stands in which each location occurred. Locations separated by  $\geq 12$  hours were spatially independent (Katnik et al. 1994, Phillips 1994); thus, we used consecutive locations of individual marten that were separated by  $\geq 12$  hours.

### Home Ranges

We defined nonjuveniles as marten  $\geq 1$  year of age and residents as marten with  $\geq 25$  locations collected during  $\geq 3$  months. For each resident, nonjuvenile marten, we calculated 95% MCP home ranges (Mohr 1947, White and Garrott 1990) using a program (SCREENER) developed by Chapin (1995). The program iteratively resampled all possible combinations of 95% of the locations to determine the combination that resulted in the smallest MCP (White and Garrott 1990:152). By removing 5% of lo-

cations simultaneously, SCREENER was able to detect groups of outliers that together contributed to a greater change in home-range area and shape than individual locations (White and Garrott 1990:151–152). Based on area-observation curves (Odum and Kuenzler 1955), Phillips (1994) determined that, for marten on our study site,  $\geq 25$  locations per animal were needed to compute home-range areas that were independent of sampling intensity (Odum and Kuenzler 1955).

### Habitat Database

We delineated the boundary of our habitat database to include an area that we estimated could be occupied by marten captured along a road and trail system on our study site. The maximum distance from potential trap locations to the boundary of our habitat database was 2.6 km, which was less than the maximum diameter (2.7 km) of marten home ranges (Phillips 1994; Fig. 1). The habitat database was developed from 1:15,840-scale color infrared aerial photographs, flown and interpreted by James W. Sewall Company (Old Town, Me.). We used a geographic information system (PC ARC/INFO 3.4.1, Environ. Systems Res. Inst., Redlands, Calif.) to integrate habitat and telemetry data. Habitat polygons were delineated based on species composition, height, and closure of the tallest vegetation layer with  $>10\%$  closure and were used to develop forest types for use in selection analyses (Table 1). We classified stands as spruce-budworm mortality (Table 1) if canopy height was  $>12$  m with 10–50% canopy closure or  $<12$  m but not wetlands or human-created openings. This classification was based on the disturbance history of our study site and extensive ground verification. Open wetlands, open water, and clearings around buildings composed only 3.5% of the study area, were considered unsuitable habitat, and were excluded from analyses.

### Habitat Selection Analysis

We tested whether marten used forest types disproportionately from availability within their home ranges (stand scale) during summer (1 May–31 Oct) and winter (1 Nov–30 Apr). For each resident nonjuvenile marten, we defined use of each forest type as the proportion of locations in that forest type. We defined availability as the proportion of each forest type within each marten's home range. We calculat-



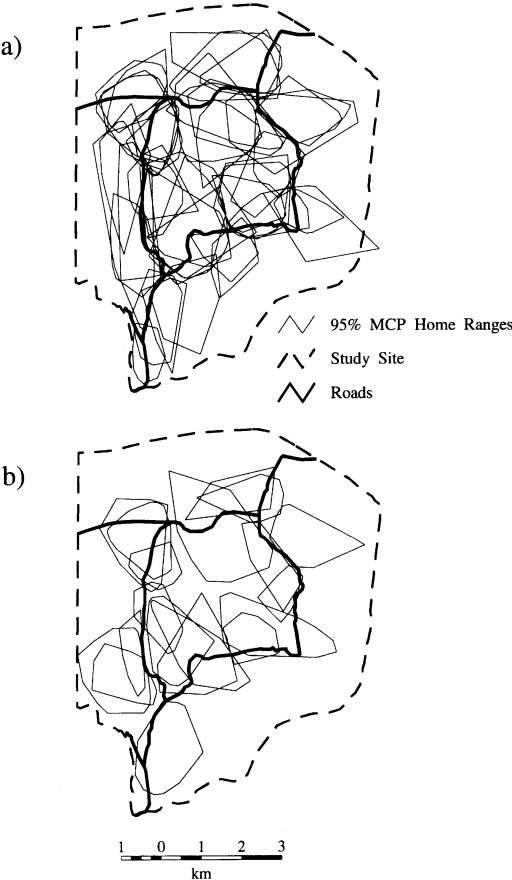


Fig. 1. Home ranges (95% min. convex polygon) of a) male ( $n = 20$ ) and b) female ( $n = 18$ ) resident, nonjuvenile ( $\geq 1$  YR) marten in northcentral Maine, 1990–94. Home ranges shown are pooled across seasons and years.

ed a selection index as use ( $U$ ) minus availability ( $A$ ) divided by availability ( $[U-A]/A$ ) for each forest type. Treating each marten as a replicate, we then ranked the forest types for each marten based on the value of the selection index. For individuals monitored  $>1$  year, we calculated selection indices separately for each year and used the mean index across years. We tested the null hypothesis that the sum of the selection index ranks across marten was equal for all forest types using the Friedman test (Conover 1980:299–305, Alldredge and Ratti 1986). If the null hypothesis was rejected, we used Fisher's least-significant-difference procedure on ranks to determine, on a pairwise basis, which habitats differed in selection indices (Conover 1980: 300, Alldredge and Ratti 1986). For the multiple comparison procedure, we used a pairwise rejection level  $= \alpha/k$ , where  $\alpha = 0.05$  and  $k =$

Table 1. Percent of study area composing forest types based on forest cover type, tree height (m), and canopy closure (%) used to evaluate seasonal stand-scale habitat selection by resident marten in northcentral Maine, 1990–94.

Forest type	Forest cover type <sup>a</sup>	Tree ht	Canopy closure	% Study area
Spruce-budworm mortality	S, SH, HS, H	>12	10–50	25.7
	S, SH, HS, H	<12	0–100	
Mature, well-stocked				
Coniferous	S	>12	>50	14.6
Deciduous	H	>12	>50	32.6
Mixed	SH, HS	>12	>50	23.6
Unsuitable	other <sup>b</sup>	<6	0	3.5

<sup>a</sup> S =  $>75\%$  coniferous, H =  $>75\%$  deciduous, SH = 50–75% coniferous, HS = 50–75% deciduous.

<sup>b</sup> Includes open water, open wetlands (e.g., beaver flows, bogs), and human-created openings (e.g., camps, gravel pits). This type was excluded from all analyses.

6 possible comparisons (Miller 1981:67–69). We used a MANOVA to test for an effect of sex, age, and a sex-age interaction on the selection indices of the 4 forest types. The 2 age classes we considered were yearlings (1 YR) and adults ( $\geq 2$  YR). If no sex, age, or interaction effect was detected, we combined data across age and sex classes before using the Friedman test. To further assess the effect of age on home range occupancy relative to habitat composition, we tested whether the amount of coniferous or deciduous forest within home ranges differed between yearlings and adults for both male and female marten, using Mann-Whitney tests (Conover 1980:216–223).

Previous studies have used the Friedman test with a selection index calculated as use minus availability ( $U-A$ ; Alldredge and Ratti 1986). This selection index is dependent upon the abundance of the respective forest type and may result in misleading conclusions regarding rare or very abundant forest types (McLellan 1986). Dividing this index by availability ( $[U-A]/A$ ; Manly et al. 1993) accounts for the relative amount of the forest type. We used the Friedman test with the individual animal as the sampling unit (Alldredge and Ratti 1986) to avoid pseudoreplication resulting from pooling locations across individuals and to allow for variability in selection among individuals. Further, we measured both use and availability of habitat within home ranges to allow for interpretations regarding the scale of habitat selection (Johnson 1980).

Table 2. Percentage of forest types within versus outside of home ranges of resident, nonjuvenile ( $\geq 1$  YR) marten ( $n = 20$  M, 18 F) in northcentral Maine, 1990–94.

Forest type <sup>a</sup>	M		F		Both sexes	
	In <sup>b</sup>	Out <sup>c</sup>	In	Out	In	Out
BWK	25.1	29.3	23.6	29.3	25.5	28.8
MWC	12.4	19.7	14.0	16.1	13.6	17.9
MWD	38.5	25.7	37.7	30.3	37.2	27.4
MWM	24.0	25.2	24.6	24.3	23.7	25.9

<sup>a</sup> BWK = severe spruce-budworm mortality; MWC = mature, well-stocked coniferous; MWD = mature, well-stocked deciduous; MWM = mature, well-stocked mixed.

<sup>b</sup> Composition of forest types in the area occupied by radiocollared marten.

<sup>c</sup> Composition of forest types in the portion of our study area that was not occupied by resident marten. This area may have been occupied by resident marten that we did not monitor.

RESULTS

We used 2,529 telemetry locations of 20 male and 18 female resident ( $\geq 25$  locations collected during  $\geq 3$  months), nonjuvenile marten that occurred within 95% MCP home ranges and had error polygons  $< 10$  ha. During summer (1 May–31 Oct), 1,495 locations were obtained from 18 males and 831 locations were obtained from 17 females. Nine males and 1 female were monitored  $> 1$  summer. During winter (1 Nov–30 Apr), 203 locations were obtained from 7 males and 1 female. The mean error polygon among ground locations was 3.5 ha ( $n = 1,317$ ), compared with the mean habitat polygon size of 11.0 ha ( $n = 483$ ). Seventy-three percent of all locations ( $n = 2,529$ ) were within 400 m of a road, an area that included only 32% of the study area. Habitat composition of areas  $< 400$  m from roads was similar to that of areas  $> 400$  m from roads (26.0 vs. 26.9% for spruce-budworm mortality, 12.1 vs. 16.5% for coniferous forest, 37.4 vs. 32.2% for deciduous forest, and 24.4 vs. 24.4% for mixed forest); thus, we included the entire study area in our habitat assessment. The fates of individual marten used in this study are discussed by Hodgman et al. (1997).

At the landscape scale, resident, nonjuvenile marten occupied nearly all of the available habitat over the course of our study (Fig. 1; Phillips 1994). We could not assume that portions of our study site lacking home ranges of radiocollared marten were unoccupied because our trapping effort was focused primarily along roads; areas lacking marten home ranges were relatively farther from roads than were areas that included home ranges (Fig. 1). Although this shortcoming precluded statistical comparisons of use ver-

Table 3. Multiple pairwise comparisons between rank sums<sup>a</sup> of selection indices among 4 forest types for 18 male and 17 female resident, nonjuvenile ( $\geq 1$  YR) marten during summer (1 May–31 Oct) in northcentral Maine, 1991–93.

Forest type <sup>b</sup>	Rank sum	vs.	Forest type	Rank sum	P-value <sup>c</sup>
BWK	104		MWC	87	0.108
BWK	104		MWD	87	0.108
BWK	104		MWM	72	0.003
MWC	87		MWD	87	1.000
MWC	87		MWM	72	0.156
MWD	87		MWM	72	0.156

<sup>a</sup> Sum of rank of habitat selection index among 4 forest types, across 35 resident marten (18 M, 17 F).

<sup>b</sup> BWK = severe spruce-budworm mortality; MWC = mature, well-stocked coniferous; MWD = mature, well-stocked deciduous; MWM = mature, well-stocked mixed.

<sup>c</sup> Bonferroni pairwise rejection level = 0.008 ( $\alpha = 0.05$ , 6 comparisons).

sus availability at the landscape scale, the high proportion of our study site within home ranges of resident marten of both sexes during the 3-year period, combined with similar habitat composition within versus outside of documented home ranges (Table 2), strongly suggests that marten within the forest preserve did not locate their ranges in areas differing in forest type composition from the available landscape.

At the stand scale, we detected no effect of sex (Wilks' lambda = 0.975,  $P = 0.909$ ), age (Wilks' lambda = 0.926,  $P = 0.548$ ), or sex-age interaction (Wilks' lambda = 0.949,  $P = 0.722$ ) on the selection indices of the 4 forest types during summer (1 May–31 Oct); therefore, we combined data across sex and age classes. During summer, at the stand scale, marten used forest types disproportionately from availability within their home ranges ( $F = 3.11$ ; 3, 102 df;  $P = 0.03$ ). Stands with severe spruce-budworm mortality had the highest selection index, which was significantly higher than that for mature, well-stocked, mixed forest ( $t = 3.05$ , 102 df,  $P = 0.003$ , pairwise rejection level = 0.008; Table 3). No other differences in selection indices were significant among all possible pairwise comparisons ( $t \leq 1.62$ , 102 df,  $P \geq 0.11$ , pairwise rejection level = 0.008; Table 3) during summer.

Based on combined data for 7 males and 1 female with  $\geq 25$  locations collected during  $\geq 3$  months, no selection at the stand scale was detected during winter ( $F = 0.26$ ; 3, 24 df;  $P = 0.83$ ). Because individual animals were treated as the sampling unit, this test suffered from potentially low power. Therefore, we pooled win-

Table 4. Median, minimum, and maximum percent of forest types within MCP home ranges of individual resident, nonjuvenile ( $\geq 1$  YR) male and female marten during summer (1 May–31 Oct) and winter (1 Nov–30 Apr) in northcentral Maine, 1990–94.

	Forest type <sup>a</sup>							
	BWK		MWC		MWD		MWM	
	M	F	M	F	M	F	M	F
Summer								
<i>n</i>	18	17	18	17	18	17	18	17
Median	23.0	20.5	9.7	9.7	41.9	37.2	22.5	22.0
Minimum	8.9	8.1	5.1	0.8	7.7	6.3	0.2	6.7
Maximum	74.1	67.2	26.2	36.3	65.3	66.1	55.9	61.0
Winter								
<i>n</i>	7	1	7	1	7	1	7	1
Median	13.5	17.7	11.7	6.5	51.6	20.2	23.4	55.7
Minimum	5.9		3.8		13.3		6.9	
Maximum	61.4		24.4		61.9		32.1	

<sup>a</sup> BWK = spruce-budworm mortality; MWC = mature, well-stocked coniferous; MWD = mature, well-stocked deciduous; MWM = mature, well-stocked mixed.

ter locations ( $n = 366$ ) among 12 males and 12 females that had  $<25$  locations during winter, but which exhibited evidence of residency (Chapin 1995). The proportion of this pooled sample of locations that occurred in coniferous (0.14) and deciduous (0.36) forest during winter did not differ from the proportion of the study site in coniferous (0.15) and deciduous (0.34) forest; simultaneous 95% confidence intervals (Miller 1981:216–217) around the observed proportion included the proportion in the study site for both types.

Most (9 of 10) resident, adult female marten were lactating when captured in late spring (D. Phillips and D. Harrison, unpubl. data), despite that only 3–36% (median = 10.5%) of their home ranges were composed of mature coniferous forest. We detected no difference in the amount of coniferous ( $P = 0.374$ ) or deciduous ( $P = 0.424$ ) forest in the home ranges of yearling ( $n = 8$ ) and adult ( $n = 10$ ) females. Similarly, neither the amount of coniferous ( $P = 0.896$ ) nor deciduous ( $P = 0.694$ ) forest differed between home ranges of yearling ( $n = 5$ ) and adult ( $n = 15$ ) males. Therefore, we present the median and range of home range composition for yearling and adult marten combined (Table 4).

The amounts of each forest type in home ranges varied considerably among individual marten of both sexes during summer and winter (Table 4). Mature, well-stocked coniferous forest was the least abundant forest type in home ranges of both sexes in both seasons and composed 0.8–36.3% of all marten ranges during summer (median = 9.7%) and 3.8–24.4% of all

marten ranges during winter (median = 11.7%). Mature, well-stocked deciduous forest was the most abundant forest type in marten ranges, composing 6.3–66.1% of all marten ranges during summer (median = 42.0%) and 8.5–49.6% of all marten ranges during winter (median = 47.6%).

DISCUSSION

Forest Age and Species Composition

We observed no evidence that marten distribution was related to coniferous forest cover on the landscape. Within home ranges of resident marten (stand scale), we detected no significant differences in selection indices during summer among mature ( $>12$  m ht), well-stocked ( $>50\%$  closure of overstory canopy) stands of coniferous, deciduous, or mixed forest types. Similarly, stand-scale selection indices did not differ significantly among mature, well-stocked forest types during summer on an adjacent industrial forest site (Katnik 1992).

Marten have been postulated to exhibit stronger preference for late-successional, conifer-dominated forests during winter than during summer (Buskirk and Powell 1994:289). Functional relations that support this hypothesis include higher visibility to predators on a snow surface (Buskirk and Powell 1994:292) and greater reliance on woody structure near the ground, which provides thermoneutral resting sites (Buskirk et al. 1989) and access to subnivean prey (Sherburne and Bissonette 1994). Limited empirical evidence from other sites suggests that marten may select more strongly



for conifer forests during winter (Campbell 1979, Soutiere 1979, Steventon and Major 1982), presumably because structural features were limiting in other habitats (Wilbert 1992). Our results are contrary to the hypothesis that mature conifer forests with closed overstory canopy are required by marten during winter. At the stand scale, we detected no significant differences in selection indices among coniferous, deciduous, or mixed forest types by resident marten during winter, and pooled locations of 24 resident marten obtained during winter indicated use of coniferous and deciduous forest types in proportion to the occurrence of those types on our study site. In addition, resident marten on our study site exhibited high winter survival (Hodgman et al. 1997) and no seasonal shift in home range location (Phillips 1994). Further, nearly all resident, adult female marten captured during spring were lactating, despite that several females occupied home ranges with little coniferous habitat during winter. Although marten may prefer habitat with overhead cover and structure near the ground during winter, our data indicate that, within home ranges, these requirements were met in a variety of habitat types, including mature deciduous-dominated forest and forest regenerating from spruce-budworm mortality.

We did not detect selection among our 4 forest types at the landscape scale. However, Katnik (1992:136) reported significant landscape-scale selection during summer for mature mixed forest over mature coniferous and deciduous forest as well as for forest >6 m in height over regenerating (<6 m ht) and recently-cut forest. Further, we observed stand-scale selection for stands with substantial spruce-budworm mortality over mature mixed stands, whereas Katnik (1992) detected no stand-scale selection. The disparity in these results from adjacent study sites likely relates to differences in the silvicultural management of the 2 sites. Extensive salvage cutting and pesticide spraying (Ireland et al. 1988) greatly reduced the amount of spruce-budworm mortality in the managed landscape studied by Katnik (1992) relative to our site, where no spruce-budworm management occurred. These naturally disturbed stands were characterized by increased numbers of snags, windfalls, and root mounds relative to areas that regenerated following clear-cutting. Regenerating clearcuts in the industrial forest were generally characterized by relatively

small amounts of CWD, resulting from whole-tree harvesting and roadside delimbing. Insufficient CWD may contribute to the apparent avoidance of recently cut and regenerating forests by marten when they establish home ranges. Further research is needed to define and quantify the specific amounts and types of CWD or other stand features that may be required to provide adequate forest structure for marten.

Landscape-scale selection (Katnik 1992), combined with intensive trapping (Hodgman et al. 1994), contributed to a lower density of marten in an adjacent industrial forest relative to our site (Phillips 1994). Within the industrial forest, home ranges of resident marten occupied less than one-third of the available landscape (Phillips 1994), annual trapping mortality exceeded 50% for all age-sex cohorts (Hodgman et al. 1994), and 45% of the landscape comprised recently-cut or regenerating clearcuts (Katnik 1992:68). Further, residual forest patches (overstory >6 m ht) composed a large proportion of the home ranges of resident males and females monitored in the industrial forest, and used residual patches were larger and less isolated than unused patches (Chapin 1995). In contrast, home ranges of radiocollared marten within our forest preserve site occupied most of the available landscape (Phillips 1994; Fig. 1) and comprised a wide range of different forest types (Table 4). Because trapping-induced changes in density could have confounded comparisons of habitat selection between sites (Van Horne 1983), Phillips (1994) compared indices of marten population performance between our forest preserve site and the industrial forest site. He detected no significant differences in percent lactating, home range area, or degree of intrasexual overlap between resident adult females in the forest preserve and in the adjacent industrial forest. His findings suggest that via landscape-scale selection for patches of predominantly residual forest, marten occupying patchy mosaics in logged landscapes may maintain productivity comparable to marten in unlogged landscapes if trapping harvests are managed conservatively and if residual forests (>6 m ht) that exceed the area requirements of marten are maintained.

### Selection for Overstory Canopy

Marten select for closed-canopy forests (Koehler and Hornocker 1977, Soutiere 1979,

Spencer et al. 1983, Bateman 1986) throughout their geographic range, suggesting that marten require overstory canopy closure >30% and prefer canopy closure >50% (Allen 1982, Thompson and Harestad 1994:357). Results from our study are inconsistent with this paradigm. Stands with significant mortality from spruce budworm had the highest selection ranking, despite canopy closure of mature trees (>12 m ht) that was always <50%, and was typically <30%. In these stands, a young (10–20 YR), regenerating understory of deciduous and coniferous vegetation, an abundance of snags, and an apparent high volume of fallen dead trees and root mounds provided both vertical and horizontal structure. Such structure has been associated with habitat quality for small rodents (Miller and Getz 1973) and snowshoe hares (*Lepus americanus*; Litvaitis et al. 1985), which compose significant components of the diet of marten in Maine (Soutiere 1979). During winter, these structural features also may increase opportunities for access to subnivean prey and resting sites (Corn and Raphael 1992).

Previous researchers have postulated that overstory canopy closure provides marten with escape cover, especially from avian predators; however, only one of 8 occurrences of predation on our study site was attributable to an avian predator, whereas 6 of 8 occurrences of predation were documented to be by mammals (Hodgman et al. 1997). Overhead cover from avian predators, if required, could be provided by regenerating trees, tall herbaceous growth, and CWD, as well as by mature trees. Such structure near the ground also could provide opportunities for marten to escape from terrestrial predators such as fisher (*Martes pennanti*) and coyotes (*Canis latrans*; Hodgman et al. 1997). We believe that structural requirements of marten, although sometimes correlated with stand age and canopy closure, could be maintained in a variety of managed and unmanaged stands without a closed overstory canopy of mature trees.

## MANAGEMENT IMPLICATIONS

Our results are consistent with the hypothesis that vertical and horizontal structure may be more important habitat attributes than age or species composition of the forest overstory (Buskirk and Powell 1994:286, Buskirk and Ruggiero 1994:22, Katnik 1992). Structurally complex habitats, although sometimes correlat-

ed with stand age and species composition, may be present in a variety of managed and unmanaged stands. Because factors influencing structural conditions (e.g., silvicultural history, fire history, insect damage, moisture, topology, aspect) are site specific and tree species vary greatly throughout the geographic range of the marten, we suggest that specific structural thresholds be quantified to describe marten habitat suitability. Structurally based assessments of marten habitat might include variables associated with stand age or tree species (e.g., diam. of CWD), but should not include specific tree species or stand-age requirements as predictors of marten occurrence or density.

Our results indicate that marten may neither prefer nor require conifer-dominated forests or forests with a closed overstory canopy throughout all of their geographic range. Previous reports that marten prefer or require a coniferous habitat component (Francis and Stephenson, 1972, Taylor and Abrey 1982, Spencer et al. 1983, Wynne and Sherburne 1984, Bateman 1986) may result from less structural diversity near the ground in deciduous relative to coniferous forests in some parts of the western United States, from confounding influences of analytical approach and scale in quantifying habitat selection, or from failure to address habitat components other than overstory species composition. Because of the regional and site-specific nature of relations between forest structure, species composition, age, and overstory closure, we recommend that conservation practices for marten account for the wide range of habitats occurring throughout the species' occupied range and focus on structural attributes that functionally influence the quality of forested habitats for marten, rather than merely age, species composition, and canopy closure of overstory trees.

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